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STUDIES ON THE VEGETATION DYNAMICS OF NANOCYPERION COMMUNITIES III. ZONATION AND SUCCESSION

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Abstract

Using the "degree of succession" (DS) index of Numata, as with the descriptions in Parts I. and II. of this study, the succession types in the upper and lower parts of the Nanocyperion zone can be distinguished. The vegetation of the upper Nanocyperion zone shows a successive relationship with the Bidentetea associations of the higher level, as does the vegetation of the lower zone with the Agropyro-Rumicion associations of the higher flood-plain levels. The transition in the direction of the Agropyro-Rumicion associations is represented by the cyperetosum fusci subassociation of the *Rorippo-Agrostietum stoloniferae* association, first described in the present paper.

Introduction

The rapid changes characteristic of the Nanocyperion (now referred to as Elatini-Eleocharition ovatae Pietsch 65) zone of the river-bed — by the term Nanocyperion zone we mean the bed section where the Nanocyperion species appear with a considerable coverage and which forms a more or less definite zone, even if only for a short period — take place in a manner difficult to interpret cenosystematically and which has not yet been completely clarified. This is referred to by the complicated cenosystematic network of the associations, subassociations and varieties found in this zone. The cenotaxa belonging here (which deserves a mention) can be classed among the Nanocyperion flavescentis W. Koch 26, Chenopodion fluviatile Tx. 60. Bidention tripartitae Nordh. 40, and Agropyro-Rumicion crispi Nordh. 40 association groups, by which means three association classes (Isoëto-Nanojuncetea Br.-Bl. et Tx. 43, Bidentetea tripartitae Tx., Lohm., Prsg. 50, and Plantaginetea majoris Tx. et Prsg. 50) account for the population of a relatively small part of the river-bed.

The studies performed so far (Bagi 1985, Bagi—Körmöczi 1986) with the help of multivariate methods have distinguished two kinds of populations found in the lower zones of the Körös-bed: the "exterior" primary succession taking place in higher reliefs and the "interior" primary succession in the deeper reliefs, closer to the water. The populations of differing types have been verified by the multivariate analysis of both the species and the cenoses.

Historical relations

The botanical analysis of the river-bed was restricted to the classification given by floralists at the beginning. Accordingly, valuable enumerations were provided by POLGÁR (1912, 1927) from the Szigetköz area of the Danube; by LÁNYI (1914, 1916) from the Csongrád county regions of the River Tisza; by BOROS (1929) and SOÓ (1938) from the areas touching the reaches of the River Tisza bordering on the Nyírség (a district in north-eastern Hungary), as well as by PRISTER (1947) from the alluvium-shallows of the Szamos in the surrounding area of Kolozsvár. An overall review of the retraceability of the earlier, rather sporadical botanical information can be obtained from the works of ZÓLYOMI (1937) and TÍMÁR (1950a, b).

The "plant-sociological", cenological studies on riverbeds began to show rapid progress in the 1930s—40s, with the application of the results of the Zürich-Montpellier School (BRAUN—BLANQUET, 1951). The studies of ZÓLYOMI (1937) on the Szigetköz paved the way. The work of ÚJVÁROSI (1940) is the first comprehensive cenological study pertaining to the region along the River Tisza. It was TÍMÁR (1943, 1948, 1950a) who studied the banks of the River Tisza most thoroughly, extending his studies to the Maros as well (TÍMÁR 1950b). His works provide an overall view of the cenological, zonational and successive relations of the mentioned rivers. Following TÍMÁR, BODROGKÖZY (1958, 1971, 1982, 1985) dealt with the vegetation of the lower zones of the River Tisza in detail. He firstly studied the pedological features of the plant communities, and his later publications comprise their hydroecological evaluation. The most complete cenosystematic summary of the Hungarian Nanocyperion associations is linked with the name of PIETSCH (1973).

However, specialist literature does not contain such a notion about the succession relations of the lower zones of the river-bed, which would give a joint interpretation of the development and presence of the association-groups mentioned in the Introduction. The most specific study of the process of succession was carried out by TÍMÁR (1950a), the theories of whom were also adopted by SOÓ (1962). TÍMÁR drew a distinction between the succession types characteristic of the sandy, silty and clayey banks. His succession-scheme for silt soil can be applied to describe, on a large scale, the vegetation along the Körös.

KÁRPÁTI et *al.* (1962) also a refer to the Agropyro-Rumicion group neglected by TÍMÁR (or, more exactly, mentioned by him for higher reliefs as the agrostidetosum stoloniferae flood-plain type) as a characteristic succession stage of the lower reliefs, but no detailed analyses were given, nor were the connections with the Nanocyperion, Bidention and Chenopodion fluviatile demonstrated.

The cenological research of the specific study area, the Körös-bed, is rather meagre, though a large number of studies have been carried out in respect to forest types. The work of MÁTHÉ (1936), however, was not followed by any major cenological publications; apart from the forest-communities, studies on other communities are almost completely missing from specialist literature. One descriptive work on the Nanocyperion associations along the Körös is the essay of TÍMÁR—BODROGKÖZY (1959) relating to Tiszazug.

Materials and Methods

The contour sketch map of the study area is found in Fig. 1. Six, well distinguishable stands are demarcated in the area. The different stands are almost horizontal, thus, their vegetation can be regarded as being of a homogeneous distribution. The relevés were made at two points in time: the

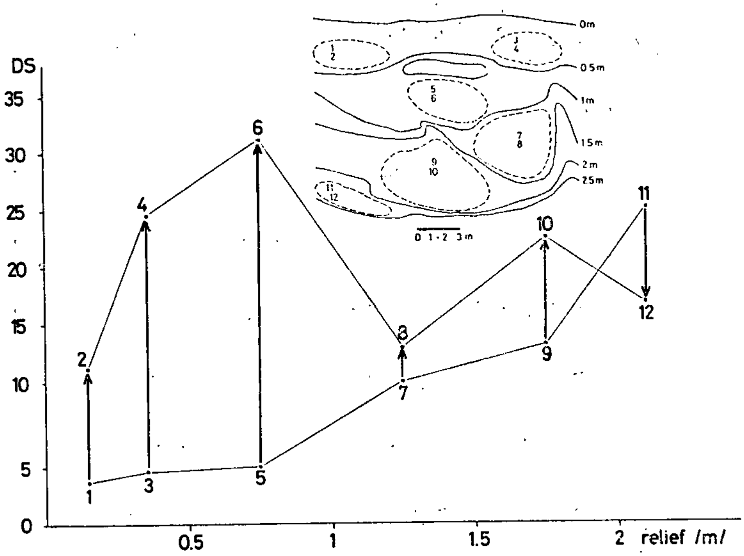

Fig. 1. DS values of the relevés as a function of the relief. The numerals correspond to the serial numbers of the cenological relevés as regards Table 1. The trend of the change of vegetation of the same stand is indicated by an arrow. The regional localization of the different relevés is shown on the complementary contour sketch map, on which a dotted line indicates the border of the stand

earlier ones (on 6th September, 1982) at the beginning of the vegetation period, shortly following inundation; the later ones at the end of the vegetation period (on 30th October, 1982), shortly before the first major autumn frost. Owing to the rapid and marked transformation of the vegetation — which makes mathematical processing possible — the estimation errors of the coverage are negligible as compared with the changes taking place in the composition of the vegetation.

To characterize the successional state of the relevés, the "degree of succession" (DS) index of NUMATA (1962) was used (ref. NUMATA 1969):

$$\mathrm{DS} = \frac{\sum^{n} ld}{n} v \tag{1}$$

where l is the number of the Raunkiaer-type life-form of the plant species (FEKETE 1981): Th=1, H and G=10, N=50, M and MM=100; d is the value characteristic of the dominance of the plant species; n is the number of species occuring in the stand; and v characterizes the total coverage of the vegetation: 100% coverage is indicated by the value 1. NUMATA (1979) published a complemented variant of his DS index, according to which:

$$\mathrm{DS} = \frac{\sum^{n} ldc}{n} v \tag{2}$$

where c is the so-called "climax adaptation number", being 1 in case of the pioneer species and 5 in case of the climax species. Since, in the given case, the majority of the species can be regarded as pioneer species, the calculations were prepared in the form of index 1. The reliability of the DS index is proved by its applications in Hungary (PAPP—PRÉCSÉNYI 1980, PRÉCSÉNYI 1981).

Results

DS values were calculated on the basis of Table 1, which, apart from the coverage data of the species, also comprises the important data of the relevés, and the life-form categorization of the plant species (Soó 1964—1980), as well as their ordered NUMATA-number.

Table 1. *Cenological data of relevés*

Life forms	Numata's numbers	Number of relevé	1	2	3	4	5	6	7	8	9	10	11	12
		Total covering (%)	20	75	20	85	30	90	60	95	70	85	85	80
		Number of species	17	30	14	28	18	20	21	28	24	31	16	21
		Nanocyperion												
Th	1	*Cyperus fuscus*	17	10	20	2	20	4	11	+	17	+	58	+
Th	1	*Dichostylis micheliana*	43	6	36	2	38	+	11	+	9	+	2	
Th	1	*Gnaphalium uliginosum*	5	17	8	5	6	9	8	+	3	+	1	5
H—HH	10	*Veronica anagallis-aquatica*	1	+	2	3	+		3	2				
Th—H	10	*Potentilla supina*		2		5		4		1		2		
H—HH	10	*Veronica beccabunga*	+	+	2	4								
HH	10	*Chlorocyperus glomeratus*		+		+	+	+						
Th	1	*Heleochloa alopecuroides*					+				1			
Th	1	*Juncus bufonius*		1										
Th	1	*Limosella aquatica*		+		+								
		Bidentetea												
Th	1	*Echinochloa crus-galli*	2	2	2	3	3	3	1	14	13	13	6	20
Th	1	*Chenopodium rubrum*	2	17	5	2	3	4	12	4	5	7	+	2
Th	1	*Polygonum lapathifolium*	1	+	2	+	3	+	15	26	3	4	+	3
Th	1	*Bidens tripartita*		1		1	+	2	1	6	+	1	+	15
Th	1	*Xanthium italicum*	3	+		2			8	6	1	1	3	10
Th	1	*Chenopodium polyspermum*	+				2		2		3			+
Th	1	*Chenopodium chenopodioides*	3	+							1	1		
Th	1	*Chenopodium ficifolium*							1	1	1	1		
Th	1	*Chenopodium glaucum*									+	+		
Th	1	*Polygonum hydropiper*								8	+	6		
Th	1	*Atriplex hastata*		+		+				+				
Th	1	*Ranunculus sceleratus*		1										

		Plantaginetea												
H	10	*Plantago major*	9	3	8	9	10	9	4	6	9	10	17	4
H	10	*Rumex stenophyllus*	2	7	4	21	2	17	1	4		4		2
H	10	*Rorippa sylvestris*	4	22	4	9	5	34	8	3	9	10	6	1
H	10	*Agrostis stolonifera*		4		+		1		+	+	6	+	10
H	10	*Tanacetum vulgare*		1		4	1	3	1	5	+	4		+
H—HH	10	*Typhoides arundinacea*											2	5
H	10	*Juncus effusus*		+	1									
		Chenopodio-Scleranthea												
H—HH	10	*Lythrum salicaria*	7	4	7	17	4	3	8	8	7	10	+	8
Th	1	*Amaranthus lividus*	+	1	+	4	2	7	2	+	3	+	2	3
H—HH	10	*Lythrum virgatum*	1	+		+		+	3	2	4	3		
Th	1	*Chenopodium album*		+		1			+	4	4	8		2
Th	1	*Amaranthus retroflexus*		+		+		+				2		2
Th	1	*Portulaca oleracea*					1	+			3	2		
Th	1	*Matricaria inodora*		+		+				+		+		
G	10	*Cirsium arvense*											+	5
Th—H	10	*Malva neglecta*										+		3
Th	1	*Sonchus asper*								+		+		
		Other species												
M	50	*Salix triandra*		1		1			+	+	4	4	3	+
HH	10	*Oenanthe aquatica*			+	4			+	+		+		
HH	10	*Lycopus europaeus*								+		+		
H	10	*Urtica dioica*						+				+		
HH	10	*Alisma lanceolatum*								+				
		Degree of succession (DS)	3.72	13.4	4.90	24.5	4.97	33.3	10.1	12.9	13.0	20.2	25.1	16.8

Table 2. *Rorippo-Agrostietum stoloniferae* (MOOR 58) OBERD. et TH. MÜLL. 61 *cyperetosum fusci* subass. nova

	Number of relevés	1	2	3	4	5	6	7	8		
	Total covering (%)	40	65	30	50	70	20	60	20		
	Number of species	20	23	16	24	36	19	23	18		
	Sampling plot (m²)	18	18	6	25	25	20	6	15		
	Date, 1982:	3.9	3.11	3.9	5.9	1.11	1.11	6.9	1.11	K	
	Ass. Character Species										
H	*Rorippa sylvestris*	2.3	2.3	2.2	2.3	2.3	3.4	3.4	2.2	V	2.2—3.4
	Subass Diff. Species I. Nanocyperion										
Th	*Cyperus fuscus*	2.2	2.1	3.2	2.1	1.1	2.1	2.2	2.1	V	1.1—3.2
Th	*Gnaphalium uliginosum*	2.2	1.1	2.1	1.1	1.1	1.1	1.1	1.1	V	1.1—2.2
Th	*Dichostylis micheliana*	1.1	1.1		2.1	1.1	+	2.1	2.1	IV	1.1—2.1
Th	*Heleochloa alopecuroides*	+	+	1.1				+		IV	+—1.1
Th—H	*Potentilla supina*		+						+	II	+
Th	*Juncus bufonius*		1.1							I	1.1
Th	*Limosella aquatica*								2.1	I	2.1
	Subass. Diff. Species II. Agropyro-Rumicion										
H	*Rumex stenophyllus*				+	2.3	2.2	1.2	2.3	IV	+—2.3
H	*Rumex crispus*	+	2.3	2.3	2.2	2.3				IV	+—2.3
	Agropyro-Rumicion										
H	*Agrostis stolonifera*	+	2.2	1.1	+	1.1	+	1.1	1.1	V	+—2.2
H	*Tanacetum vulgare*		1.1			+		1.1	+	III	+—1.1
Th	*Rorippa palustris*		+			1.1				II	+—1.1
H	*Juncus effusus*				1.1	+				II	+—1.1
G	*Juncus compressus*			1.1						I	1.1
	Plantaginetea										
H	*Plantago major*	2.2	2.2	2.1	1.1	1.1	2.2	2.2	2.3	V	1.1—2.3
HH	*Rorippa amphibia*				1.2	1.1				II	1.1—1.2

	Bidentetea										
Th	*Chenopodium rubrum*	1.2	1.2	+	2.2	1.2	1.1	1.2	1.2	V	+—2.2
Th	*Echinochloa crus-galli*	1.2	1.1	2.2		1.2	1.2	1.2	+	V	+—2.2
Th	*Xanthium italicum*	1.1	1.1	1.1	1.3	1.2	1.1	1.1	1.2	V	1.1—1.3
Th	*Polygonum lapathifolium*	1.2	1.1	2.2	1.1	1.1		1.1		IV	1.1—2.2
Th	*Bidens tripartita*	+	1.1		1.1	1.2		1.1		IV	+—1.2
Th	*Chenopodium ficifolium*	1.1	+	1.1			2.2	+		IV	+—2.2
Th	*Atriplex hastata*	+		+		1.1	1.1		1.2	IV	+—1.2
Th	*Ranunculus sceleratus*		+		1.1	1.2	+		1.2	IV	+—1.2
Th	*Polygonum hydropiper*			1.2	1.2	1.1		+		III	+—1.2
Th	*Chenopodium polyspermum*					1.1				I	1.1
	Chenopodio-Scleranthea										
H—HH	*Lythrum salicaria*		+		2.2	1.1		2.3	1.1	IV	+—2.3
Th	*Portulaca oleracea*	3.2	3.2	1.1		+		+		IV	+—3.2
Th	*Amaranthus lividus*				+	+	+	+		III	+
Th	*Amaranthus retroflexus*	+	+			1.1			+	III	+—1.1
Th	*Chenopodium album*	+	+				1.1			II	+—1.1
Th	*Sonchus asper*		+			1.1	+			II	+—1.1
G	*Cirsium arvense*				1.1	1.1				II	1.1
Th	*Capsella bursa-pastoris*					1.1				I	1.1
	Other species										
M	*Salix triandra* (j)	+	+		1.1	1.1	2.1	+		IV	+—2.1
HH	*Oenanthe aquatica*				+		+		1.2	II	+—1.2

Bolboschoenus maritimus 2+; *Chlorocyperus glomeratus* 7+, 4+; *Chenopodium chenopodioides* 1+, 7+; *Chenopodium glaucum* 6+; *Cyperus difformis* 4+; *Lysimachia vulgaris* 3+, 5+; *Malva neglecta* 5+; *Matricaria inodora* 6+; *Mentha arvensis* 5+; *Plantago lanceolata* 2+; *Solanum dulcamara* 5+; *Taraxacum officinale* 4+, 5+; *Urtica dioica* 5+; *Veronica beccabunga* 7+.

The results illustrated as a function of the relief are shown in Fig 1. The DS values of the relevés taken on the earlier date increase with the raise in relief, the cause of which is that the vegetation had longer periods at disposal for development with an elevation in relief, which mainly led to the increase in total coverage. Characteristic of the species composition is that the Nanocyperion character species are dominant at lower reliefs (1., 3., 5. relevés), while, at higher reliefs (7., 9. relevés), the Chenopodio-Scleranthea and, within this, the Bidentetea and Plantaginetea character species appear with a considerable coverage, besides the Nanocyperion species. In these relevés the species number is somewhat higher. It is also a Nanocyperion species, the *Cyperus fuscus,* that dominates in the 11. relevé. The low coverage ratio of the Chenopodio-Scleranthea character species can be traced back to competitive elimination arising as a consequence of the large coverage of the rapidly spreading *Cyperus fuscus,* which, due to the great moisture content of the soil, may be considerable at the beginning of the vegetation period. The differing species composition of the 7. and 9. relevés is also caused by the circumstance that the two relevés belong to that zone of the river-bed where large amounts of organic matter and debris are deposited by the surf of the river. Therefore, the appearance of the Bidention character species in a higher ratio is a regular feature here. The deposition of organic debris at higher (11. relevé) and reliefs is to a lesser degree.

In case of the relevés recorded at the later point in time, the development of the DS value is sharply divided into two parts. At the lower relief (2., 4., 6. relevés) the DS value shows a marked increase with the elevation of the relief. The increase in DS is in connection with the greater coverage and the appearence of the species having a H, H—HH life-form. These factors can compensate for the decrease in the DS value arising from the increase in species number. At higher reliefs (8., 10., 12. relevés) the increase in DS value is of a slighter degree and is even decreasing in case of the 12. relevé. Such a change in the DS value is caused mainly by the increase in species number, as well as by the fact that, besides the almost unchanged value of the total coverage, Bidentetea instead of Nanocyperion species appear, though both are of Th life-form.

Cenosystematic evaluation

At higher reliefs the first to develop is the Nanocyperion, mainly the *Cypero-Juncetum* association, which can also appear in an almost typical form (11. relevé). In the zone where the organic debris accumulates, the appearance of the Bidentetea species follows shortly after — almost simultaneously with — these Nanocyperion species (7., 9. relevés), which are partly Bidention tripartitae, partly Chenopodion fluviatile character species. With the advanced vegetation period, the soil of the higher reliefs becomes dry, which is unfavourable for the Nanocyperion species sensitive to a lack of water. Hence, their predominance shows a considerable decrease in the cenoses (8., 10., 12. relevés). The degradation of their cenoses is evident, most strikingly, in the decrease in DS value in the 11., 12. relevés. The free areas can be occupied by the Bidentetea species (cf. Soó (1964—80) I. vol., p. 218, Soó (1957), p. 339).

At lower reliefs, the earlier relevés comprise the character species of both the *Cypero-Juncetum* and the *Dichostylidi-Gnaphalietum* associations, in correlation with the fraction-composition of the soil on the Körös-bed (cf. Kárpáti 1985), since, in the lighter soil of the river-bed, the *Cypero-Juncetum,* while, in the bound soils, the *Dichostylidi-Gnaphalietum* are the more characteristic associations. From this point of view, the soil in the studied reach of the Körös is of an intermediate type. Thus, the development of the two communities here either forms mosaic-complexes, or transitions of each other (Fig. 2). According to BODROGKÖZY (1982), the decisive factor is the distribution of the seeds in the soil.

With the advancement of the vegetation period, there is a considerable increase in the vegetation coverage. At the same time, the moisture of the soil does not decrease essentially due to proximity of the water level of the river. Such species appear

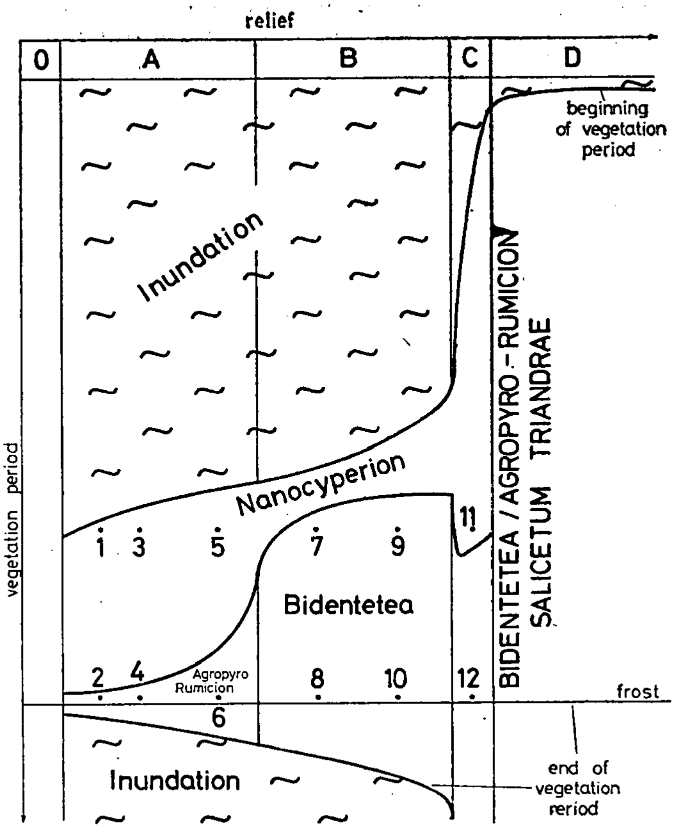

Fig. 2. A soil-fraction analysis of the soil-segments of the study area. The dominant fraction is the silt fraction. The percentage distribution of the soil grains between the clay and sand fractions is of an identical order of magnitude. The clay fraction is approximately double that of the sand fraction. The horizontal axis shows the percentage share of the fraction indicated in the heading from the whole soil sample, to the depth interval displayed on the left

which develop more slowly beside the Nanocyperion species, but have greater competitive ability and hinder the further increase in coverage of the Nanocyperion species. These species are partly of a Chenopodion fluviatile (2. relevé), partly of an Agropyro-Rumicion character (4., 6. relevés). Therefore, in the deepest zone of the river-bed — in case of the vegetation period being enough — there is the possibility for their appearance, which is otherwise characteristic of the relief above the Bidentetea associations (found in the Nanocyperion zone of the river-bed) (KÁRPÁTI et *al.*, 1965). The higher succession grade is indicated by the high DS value of the 6. relevé.

The Agropyro-Rumicion stand developing here differs from the Agropyro-Rumicion associations found on the higher areas in many essential aspects.

The stand is mainly similar to the *Rorippo (sylvestri)-Agrostietum stoloniferae* (MOOR 58) OBERD. et TH. MÜLL. 61. association (cf. MARKOVIĆ 1973, BODROGKÖZY 1985). An essential difference is that, as regards relief, it develops parallel with the dissociation of the Nanocyperion associations characteristic of the zone below the Bidentetea (Chenopodion fluviatile) associations. It contains a considerable amount of Nanocyperion elements, while the typical *Rorippo-Agrostietum* associations have no Nanocyperion antecedents (KÁRPÁTI—KÁRPÁTI 1963, MARKOVIĆ 1978). Its characteristic appearance can only be studied in case of an adequately long vegetation period. This, together with its transitional character, is the reason why no mention has been made up to the present. (The *Rorippo-Agrostietum stoloniferae* itself is an association which has not been known long, as it is not mentioned in the Übersicht III of SOÓ (1961). Similarly, it has extensive stands characteristic of large areas (KÁRPÁTI—KÁRPÁTI 1963)). The predominant species of the stand are the *Rorippa sylvestris* and, in typical cases, in an almost identical ratio, the *Rumex stenophyllus,* or the *Rumex crispus*. The two *Rumex* species may occur separately as well as together. The *Rumex stenophyllus* is more characteristic of the stand. A basic deviation from the *Rorippo-Agrostietum* association characteristic of higher reliefs is that the subspecies (varietas) of the *Agrostis stolonifera* prorepens occurs too. (It is also held to be a species under the name of *Agrostis stolonizans* BESS., cf. SOÓ 1964—80, V. vol., p. 399). Accordingly, the stand is markedly distinguished from its typical association by the *Agrostis stolonifera* ssp. *prorepens,* cf. BRAUN—BLANQUET (1951), p. 21.

Based on the aforementioned, cenosystematically the stand can be regarded as a *Rorippo-Agrostietum* association. The appearance of the *Rumex* species in considerable coverage points towards the *Rumici-Alopecuretum geniculati* TX. (37) 50 association. The relatively long-lasting inundation is presumedly a common environmental factor. However, the *Rumici-Alopecuretum* association is not characterized by the appearance of the Nanocyperion species (MARKOVIĆ 1973). The appearance of the Gnaphalium uliginosum and the Eleocharis acicularis in this association has also been identified by BODROGKÖZY (1985) to having a zoogenic effect. Due to the occurrence of the Nanocyperion species — which refers to a habitat basically differing from that of the *Rorippo-Agrostietum* association described so far — it is reasonable to differentiate, at subassociation level, between the stands developing in the Nanocyperion zone of the river-bed. The name cyperetosum fusci is considered appropriate, after the predominant Nanocyperion species, the *Cyperus fuscus*. The appearance of the *Rumex* species in the subassociation can be evaluated cenosystematically as facies. The relevés taken from the subassociation are contained in Table 2.

Discussion

Zonation and succession

The succession relations of the lower zones of the Körös river-bed are illustrated by the following vegetation period — relief scheme (Fig. 3).

On the basis of the idealized scheme (neglecting transitions and mixings), along an optimal horizontally drawn relief axis, it can be readed off what zones are formed by the vegetation at a given time-point on the lower parts of the river-bed. For example, at the time of the earlier plotting the relevés preapred at the deepest reliefs fall into the Nanocyperion zone, the next two into the border of the Bidentetea-Nanocyperion

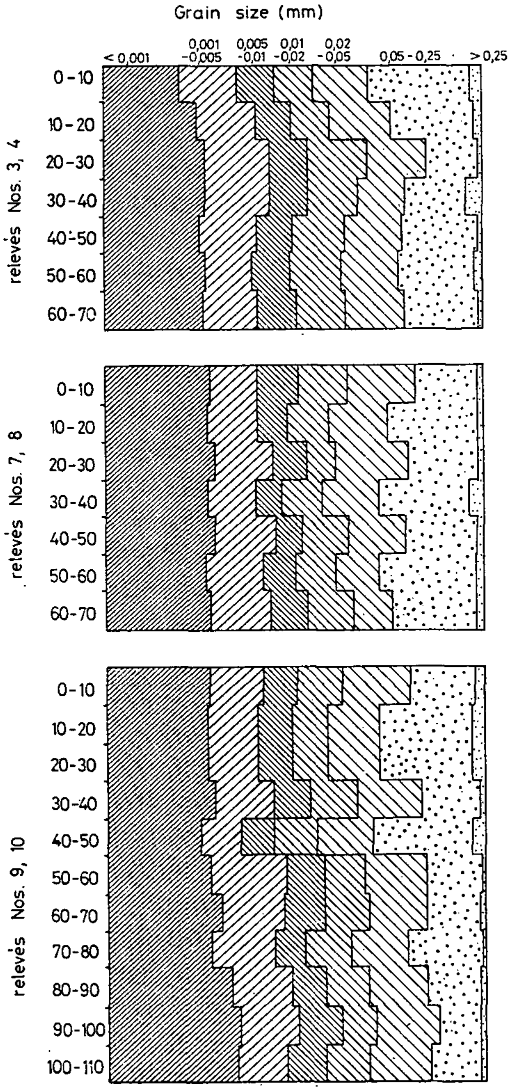

Fig. 3. The connection between zonation and succession on the lower zones of the river-bed. The vegetational period begins with the cessation of water coverage and ends frequently with the first strong frost, more rarely, with the elevation of the water level. See details in the text

zone, and the stand recorded at the hightes relief (11.) into a narrow Nanocyperion zone. The development of the vegetation in the studied section of the river-bed can be regarded as a process of succession which begins with the end of the inundation and the extension of which is hindered by the newer inundation, bringing the succession back to the starting point. The first, examinable steps of the succession are separated from each other in the lower zones of the river-bed. In the "A" zone — if sufficient time is at our disposal — the Nanocyperion associations *(Cypero-Juncetum* and *Dichostylidi-Gnaphalietum*) may develop into an Agropyro-Rumicion association, and there is the appearence of the species of the *Chenopodietum rubri* association. The succession index of these ranges from 20 to 40. The *Rorippo-Agrostietum stolonifera*e association developing on the higher levels of the river-bed is characterized by a DS value around 60—130 (KÁRPÁTI—KÁRPÁTI 1963). In the "B" zone — of which the accumulation of organic debris is characteristic — the Bidentetea associations develop after a rather short Nanocyperion phase. Here the succession has somewhat organogenic character (SIMON 1957). This is suggested by the presence of the Bidention tripartitae species (but, must be compared with cenosystematic uncertainty, as regardings the condition of the "*Xanthietum italici*" (POLI—TÜXEN 1960, SOÓ 1964—80, MARKOVIĆ 1981)). At the beginning the "C" zone is a typical Nanocyperion one. However, with the effect of the drying out caused by the decreased water level, its place is occupied by Bidentetea associations in the advanced vegetation period. The vegetation period of the grade demarcated "D" (Fig. 3) is long enough for the perennial plant species to develop closed stands. As consequence, there is no possibility here for the appearance of the Nanocyperion species.

It is apparent, from the aforementioned, that in the lower parts of the river-bed the zonation and succession cannot be brought into compliance: i.e. the vegetation of the higher zone does not signify that the next succession stage of the vegetation found in the zone below it. In this initial phase of the succession, the Bidentetea associations may not be considered as a successive transitions between the Nanocyperion and the Agropyro-Rumicion associations. This is all the more probable regarding the *Rorippo-Agrostietum cyperetosum fusci* stand developing on the lower reliefs of the river-bed. Owing to the accumulation of excess organic matter, it seems the Bidentetea associations indicate another means of succession (of a degradative character). They are probably related to the Bidentetea, and, within this, to the Bidention tripartitae associations of the higher reliefs. These conclusions are also supported by the DS values calculated according to community types. The following factors may play a role in the development of these alternative succession types of the river-bed:

1. The zonation form of soil properties;
2. Changes in humidity relations, depending on relief;
3. The specifity of the duration of the vegetation period by the relief;
4. Differences in propagulum distribution in the soil (cf. TÍMÁR 1950a for the connection between seed size and deposition, p. 89);
5. The differing growth of the species;
6. The differing tolerance of the species in respect to environmental changes;
7. The differing competitive ability of the species, which may differ from each other, to various degrees, with changes in environmental parameters;
8. The ratio of the life-time of the species and the length of the vegetation period at its disposal (WHITTAKER 1974);
9. The life-form (cf. BAGI—BODROGKÖZY (1984), under identical hydroecological conditions, in a drying out flood-plain lake, besides a sinking water level, the hemikryptophyton *Agrostis stolonifera* is displaced by the therophyton *Heleochloa alopecuroides* at deeper reliefs);
10. The possibility of migration.

The gravity of the listed factors, differing according to zones, is the cause of the differing route per zone of the processes of succession.

In the present report it was aimed to analyse the cenosystematic relations of the succession on the river-bed. The possibilities of the operativity of the mechanism and dynamism were only touched upon to the extent of a few hints. This can be realized by means of performing further studies in respect to the previously listed factors.

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Vegetációdinamikai vizsgálatok Nanocyperion jellegű növénytársulásokban III. Zonáció és szukcesszió

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Kivonat

Numata „degree of succession" (DS) indexének felhasználásával a dolgozat I. és II. részében leírtakhoz hasonlóan elkülöníthetők egymástól a Nanocyperion zóna felső és alsó részének szukcessziótípusai. A felső Nanocyperion zóna növényzete a magasabb ártéri szintek Bidentetea, míg az alsó zóna növényzete a magasabb ártéri szintek Agropyro-Rumicion társulásai felé mutat szukcessziós kapcsolatot. Az átmenetet az Agropyro-Rumicion társulások felé a *Rorippo-Agrostietum* stoloniferae asszociáció itt először leírt *cyperetosum fusci* szubasszociációja képviseli.

Ispitivanje dinamike vegetacije sa karakteristikama Nanocyperion zajadnice III. Zonacija i sukcesija

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Abstrakt

Korišćenjem indexa Numata „degree of succession" (DS) mogu se razdvojiti-slično kao što je već napisano u I i II delu-tipovi sukcesije, koje se nalaze u gornjoj i donjoj zoni Nanocyperion.

Vegetacija u gornjoj zoni Nanocyperion pokazuje sukcesijski odnos prema zajednicama na višim nivoima vodoplavnog zemljišta kao što je Bidentetea, dok vegetacija u donjoj zoni Nanocyperion pokazuje sukcesijski odnos prema zajednicama na višim nivoima vodoplavnog zemljišta, kao što je Agropyro-Rumicion. Prelaz prema zajednicama Agropyro-Rumicion pokazuje, prvi put u ovom delu opisana subasocijacija *cyperetosum* fusci, deo asocijacije *Rorippo-Agrostietum stoloniferae.*

Вегетационно-динамические исследования над сообществами растений типа Nanocyperion III. Зонация и сукцессия

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Резюме

Методом применения индекса Numata „degree of succession" (DS), как описано в I и II главах настоящей работы, разделены друг от друга типы сукцессии нижней и верхней частей зоны Nanocyperion. Растительность верхней части зоны Nanocyperion указывает на преемственную связь с сообществами более высоких уровней затопления типа Bidentetea, а растительность нижней зоны — с сообществами более высоких уровней затопления типа Agropyro-Rumicion. Впервые здесь описанная субассоциация *cyperetosum fusci* сообщества *Rorippo-Agrostietum* представляет собой переход к сообществам Agropyro-Rumicion.